AFRL-AFOSR-VA-TR-2015-0244

Modeling spatial maps inspired by the hippocampal system

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Final Report

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13. SUPPLEMENTARY NOTES

14. ABSTRACT

We propose that hippocampal networks are built upon a fundamental unit called a megamap, or a cognitive attractor map in which place cells are flexibly recombined to represent a large space. Its inherent flexibility gives the megamap a huge representational capacity and enables the hippocampus to simultaneously represent multiple learned memories and naturally carry nonspatial information at no additional cost. Our results suggest a general computational strategy by which a hippocampal network enjoys the stability of attractor dynamics without sacrificing the flexibility needed to represent a complex, changing world. We have also derived a set of necessary and sufficient conditions for a general class of systems that performs exact path integration, which provides an input to the megamap besides landmark cues. Our theory subsumes several existing exact path integration models, including the continuous attractor networks, as special cases. We have developed a reduction method for a class of asymmetric attractor networks that store sequences of activity patterns as associative memories. The reduction method may simplify analysis of

15. SUBJECT TERMS

hippocampal place cells, spatial map, cognitive map, attractor network model, continuous attractor, temporal sequence, path integration

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Final Report

AFOSR FA9550-12-1-0118

PI: Kechen Zhang

Modeling spatial maps inspired by the hippocampal system

Abstract

How the hippocampus encodes both spatial and nonspatial information at the cellular network level remains a largely unresolved problem. Spatial memory is widely modeled through the theoretical framework of attractor networks, but existing computational models can only represent spaces that are much smaller than the natural habitat of an animal. We propose that hippocampal networks are built upon a fundamental unit called a megamap, or a cognitive attractor map in which place cells are flexibly recombined to represent a large space. Its inherent flexibility gives the megamap a huge representational capacity and enables the hippocampus to simultaneously represent multiple learned memories and naturally carry nonspatial information at no additional cost. On the other hand, the megamap is dynamically stable, as the underlying continuous attractor network of place cells robustly encodes any location in a large environment given a weak or incomplete input signal from the upstream entorhinal cortex. Our results suggest a general computational strategy by which a hippocampal network enjoys the stability of attractor dynamics without sacrificing the flexibility needed to represent a complex, changing world. The hippocampal system is known to use two types of information for determining spatial location, namely, landmark cues and path integration based on self-motion (dead-reckoning). The path integration system is probably separate from the megamap itself but provides an input to the map. One key requirement for accurate path integration is path-invariant; that is, the activity of spatial neurons depends primarily on the current spatial location of the animal regardless of which trajectory it has followed to reach that position. We have derived a set of necessary and sufficient conditions for a general class of systems that performs exact path integration. Our theory subsumes several existing exact path integration models, including the continuous attractor networks, as special cases. Spatial navigation and some related problems could be conceptualized in terms of temporal sequences in the state space of the underlying neural network. Storage and retrieval of a temporal sequence in a neural network requires asymmetric reciprocal connections because symmetric connections would imply the existence of a Liaponov function whose minima correspond to stationary memory states. We have developed a reduction method for a class of asymmetric attractor networks that store sequences of activity patterns as associative memories. The reduced system is self-contained and provides quantitative information about the stability and speed of sequential memory retrieval in the original network. The reduction procedure can be summarized by a few reduction rules, which are applicable to various network models, including coupled networks and networks with time delayed connections.

Project Summary

We have obtained results in the directions as proposed in the specific aims of the original proposal and some results have exceeded the expectations of the original aims.

The primary aim of this project is to develop a theory of the *megamap*: a single, continuous attractor representation of space that extends over a large region. Cognitive map is an influential theory for the hippocampal place cells, and many previous computational models in this area are based on so-called *continuous attractor* networks which allow a continuum of stable states to represent a topographic map of the locations in an environment. One major limitation of typical earlier models is that the environment has to be very small so that each neuron in the underlying neural network represents at most a single location in that environment. More recent neurophysiological recording experiments from freely moving rats in larger rooms have shown that most place cells actually represent multiple locations in a large space. We have developed a new theory of attractor map that we call a megamap which generalizes the continuous attractor network models to hippocampal spatial representation in a large spatial region. The megamap neural network model allows flexible reuse or recombination of all the neurons to cover a huge area that is compatible with the size of an animal's natural habitat. The megamap has higher representational capacity than other known population coding schemes. No longer is there any requirement for an artificial boundary such as the walls of a box as in the old models. We show both analytically and numerically that the megamap can maintain the same decoding accuracy as the coverage area increases. We have worked out how the synaptic connection weights can be learned, how the dynamics of the network can be stabilized, and what are the mathematical conditions for a megamap to exhibit the emergent properties of a combinatorial mode of operation. Our results suggest that megamap is probably the basic building block for hippocampal representation of space.

Our results imply that the hippocampus has the capacity to stably represent large environments through one seamless attractor map, alleviating the size and rigidity constraints of existing continuous attractor models of place cells. The theory also offers a novel perspective that unites the representation of spatial and nonspatial information under the single principle of flexible cell recombinations. The megamap has implications for place cell recruitment, the functional conntectome of the hippocampus, and place cell remapping within a large environment. Using the megamap as the building block for these models instead of a single-peaked continuous attractor map eliminates the size limitations and provides the flexibility to adapt to environmental changes and to naturally incorporate nonspatial information.

Another aim of this project is to extend the megamap theory to model the incorporation of external landmark information into the internal, attractor map. The external inputs presumably come from spatial and nonspatial representations in the medial and lateral entorhinal areas, respectively. Although space is the most striking correlate of place cell activity, hippocampal pyramidal cells also respond to nonspatial stimuli, such as odors, objects, and pictures. The inherent flexibility of place cell recombinations permits the megamap to carry nonspatial information at no additional cost. The megamap is locally continuous in the sense that the patterns of active cells representing two nearby locations are similar, but the patterns become uncorrelated as the distance exceeds the place field size. Uncorrelated activity patterns may encode information about an environment in addition to the animal's spatial position. The megamap can store any pattern if its active cells have place fields at the corresponding location. This implies that a single hippocampal network can be interpreted as supporting both a continuous attractor map encoding space and a discrete set of point attractors encoding nonspatial information. This dual interpretation may potentially lead to unified theories of spatial and

nonspatial memory to account for the “where” and “what” components of episodic memory.

In this project we also aim to compare our model with alternative models. One focus is the development of a general theory of path integration. Animals are capable of navigation even in the absence of prominent landmark cues. This behavioral demonstration of path integration is supported by the discovery of place cells and other neurons that show path-invariant response properties even in the dark. That is, under suitable conditions, the activity of these neurons depends primarily on the spatial location of the animal regardless of which trajectory it followed to reach that position. Although many models of path integration have been proposed, no known single theoretical framework can formally accommodate their diverse computational mechanisms. We have derived a set of necessary and sufficient conditions for a general class of systems that performs exact path integration. These conditions include multiplicative modulation by velocity inputs and a path-invariance condition that limits the structure of connections in the underlying neural network. In particular, for a linear system to satisfy the path-invariance condition, the effective synaptic weight matrices under different velocities must commute. Our theory subsumes several existing exact path integration models as special cases, including the continuous attractor networks and the oscillatory interference model. This framework may help constrain future experimental and modeling studies pertaining to a broad class of neural integration systems.

Finally, we have studied attractor networks with asymmetric connections that allow storage and retrieval of temporal sequences of memory patterns. These systems might be relevant for sequential tasks such as path planning and navigation. A neural network with symmetric reciprocal connections always admits a Liaponov function, whose minima correspond to stationary activity patterns that are stored as memory states. Networks with suitable asymmetric connections can store and retrieve a sequence of memory patterns, but the dynamics of these networks cannot be characterized as readily as that of the symmetric networks due to the lack of established general methods. We have developed a reduction method for a class of asymmetric attractor networks that store sequences of activity patterns as associative memories. The method projects the original activity pattern of the network to a low dimensional space such that sequential memory retrieval in the original network corresponds to periodic oscillation in the reduced system. The reduced system is self-contained and provides quantitative information about the stability and speed of sequential memory retrieval in the original network. The time evolution of the overlaps between the network state and the stored memory patterns can also be determined from extended reduced systems. The dynamics reduction method developed here provides a concise characterization of the transient nonlinear dynamics of a class of asymmetric networks during sequential memory retrieval. On the one hand, the dynamics of the reduced system is completely self-contained and formally independent of the instantaneous state of the original network. Thus a reduced system can be analyzed on its own without referring to the original network. On the other hand, the two systems are linked by a compression procedure which allows the reduced system to predict the stability and the speed of sequential retrieval in the original network. The reduction method can be summarized by a few general reduction rules, which may apply to networks that may contain sparse memory patterns, asymmetric connections, time delays, and coupled subnets.

Publications

Our study of the universal conditions for path integration has led to a general theory that includes the attractor network with moving activity bump and the oscillatory interference model as special cases. The paper was submitted for publication after submission of the grant proposal and it was accepted for publication while waiting for this award (Issa and Zhang 2012). A review paper was published around the same time (Knierim and Zhang 2012). Preliminary results of our development of the megamap theory are published as abstracts (Hedrick and Zhang, 2013, 2014). A long research paper has been submitted for publication (Hedrick and Zhang 2015). Further mathematical analysis of the dynamical stability of megamap and application of the attractor theory to the biological data from the lab of Dr. J. J. Knierim are currently in preparation for publication. A study of a general dimension-reduction method for temporal sequences in attractor networks has been published (Zhang 2014).

References

J. B. Issa and K. Zhang (2012): Universal conditions for exact path integration in neural systems. *Proceedings of the National Academy of Sciences USA*, 109: 6716-20.

J. J. Knierim and K. Zhang (2012): Attractor dynamics of spatially correlated neural activity in the limbic system. *Annual Review of Neuroscience*, 35:267-285.

K. R. Hedrick and K. Zhang (2013): Megamap: Continuous attractor model for place cells representing large environments. *Society for Neuroscience Abstracts,* 578.01.

K. R. Hedrick and K. Zhang (2014): Megamap representation of large spaces: analysis of attractor states and incorporation of nonspatial memories. *Society for Neuroscience Abstracts,* 360.13.

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K. R. Hedrick and K. Zhang (2015): Megamap: Flexible representation of large spaces embedded with nonspatial information by a hippocampal continuous attractor network. Submitted.

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Modeling spatial maps inspired by the hippocampal system

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Kechen Zhang

Program Manager
The AFOSR Program Manager currently assigned to the award

James Lawton

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Reporting Period End Date

03/31/2015

Abstract

How the hippocampus encodes both spatial and nonspatial information at the cellular network level remains a largely unresolved problem. Spatial memory is widely modeled through the theoretical framework of attractor networks, but existing computational models can only represent spaces that are much smaller than the natural habitat of an animal. We propose that hippocampal networks are built upon a fundamental unit called a megamap, or a cognitive attractor map in which place cells are flexibly recombined to represent a large space. Its inherent flexibility gives the megamap a huge representational capacity and enables the hippocampus to simultaneously represent multiple learned memories and naturally carry nonspatial information at no additional cost. On the other hand, the megamap is dynamically stable, as the underlying continuous attractor network of place cells robustly encodes any location in a large environment given a weak or incomplete input signal from the upstream entorhinal cortex. Our results suggest a general computational strategy by which a hippocampal network enjoys the stability of attractor dynamics without sacrificing the flexibility needed to represent a complex, changing world. The hippocampal system is known to use two types of information for determining spatial location, namely, landmark cues and path integration based on self-motion (dead-reckoning). The path integration system is probably separate from the megamap itself but provides an input to the map. One key requirement for accurate path integration is path-invariant; that is, the activity of spatial neurons depends primarily on the

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Our study of the universal conditions for path integration has led to a general theory that includes the attractor network with moving activity bump and the oscillatory interference model as special cases. The paper was submitted for publication after submission of the grant proposal and it was accepted for publication while waiting for this award (Issa and Zhang 2012). A review paper was published around the same time (Knierim and Zhang 2012). Preliminary results of our development of the megamap theory are published as abstracts (Hedrick and Zhang, 2013, 2014). A long research paper has been submitted for publication (Hedrick and Zhang 2015). Further mathematical analysis of the dynamical stability of megamap and application of the attractor theory to the biological data from the lab of Dr. J. J. Knierim are currently in preparation for publication. A study of a general dimension-reduction method for temporal sequences in attractor networks has been published (Zhang 2014).

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Changes in research objectives (if any):

Not applicable.

Change in AFOSR Program Manager, if any:

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Extensions granted or milestones slipped, if any:

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AFOSR LRIR Number

LRIR Title

Reporting Period

Laboratory Task Manager

Program Officer

Research Objectives

Technical Summary

Funding Summary by Cost Category (by FY, $K)

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